Definition of Architectural Ideotypes for Good Yield Capacity in *Coffea canephora*

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● *Background* Yield capacity is a target trait for selection of agronomically desirable lines; it is preferred to simple yields recorded over different harvests. Yield capacity is derived using certain architectural parameters used to measure the components of yield capacity.

● *Methods* Observation protocols for describing architecture and yield capacity were applied to six clones of coffee trees (*Coffea canephora*) in a comparative trial. The observations were used to establish architectural databases, which were explored using AMAPmod, a software dedicated to the analyses of plant architecture data. The traits extracted from the database were used to identify architectural parameters for predicting the yield of the plant material studied.

● *Conclusions* Architectural traits are highly heritable and some display strong genetic correlations with cumulated yield. In particular, the proportion of fruiting nodes at plagiotropic level 15 counting from the top of the tree proved to be a good predictor of yield over two fruiting cycles.

Key words: Architectural traits, *Coffea canephora*, genetic correlations, heritability, plant architecture, yield capacity.

INTRODUCTION

The coffee tree is a perennial plant grown over a large number of years. Over its long period of production, which can stretch to around 40 years, yield cycles of 4–7 years are regulated by pruning frequency (cutting back or topping). Indeed, it is essential to prune coffee trees to maintain a sufficient fruiting volume throughout the long lifetime of the trees, and so that yield remains easily accessible (Coste, 1989). Whether trees are grown from seeds or cuttings, yield increases in the 3–4 years following planting, then stabilizes and usually begins to decrease in line with tree growth. In addition, as yields decline they also become less accessible as they are located at the top of the tree. This pattern, which is disrupted to varying degrees by alternations between successive years, has led agronomists to recommend pruning systems. Pruning is carried out every 5 years on average, but that frequency can vary from 4 to 7 years depending on the plant material used, on edapho-climatic conditions that may be more or less conducive to tree growth, and on all the cultural techniques adopted by growers (Bouharmont, 1977*a*, *b*).

One of the aims of coffee genetic improvement is to increase the productivity of cultivated areas (Bouharmont and Awemo, 1979; Bouharmont *et al.*, 1986). In order to do that, clone or hybrid yields have to be estimated by comparing them in trials. In theory, the yield value of plant material ought to be estimated from the yields cumulated over the lifetime of trees in trials. However, in practice plant breeders have to produce new clones or new hybrids without waiting for the complete results of their trials, which can take 30 to 40 years of observations. Indeed, it seems more important to optimize genetic gains by unit of time, i.e. annual genetic gains, rather than trying to find out with certainty what the trees produce over a large number of years. To do this, it is important to know the relation between yield in the early years and yield in later years (Cilas *et al.*, 2003). Moreover, traits that can be estimated at an early stage can be linked to yield in the early years, with a view to more effectively predicting later tree yields. Among the early traits, those linked to tree architecture can be used (Hallé *et al.*, 1978). Indeed, coffee tree yields are linked to the architectural development of the trees (De Reffye, 1979), i.e. there is a close relation between tree growth and yield capacity (Snoeck and De Reffye, 1980). In this study we used the quantitative approach of plant architecture first developed on coffee plants (De Reffye, 1979). Coffee trees resulting from seeds consist of an orthotropic axis; at each node, two plagiotropic branches develop, following an opposite-decussate phyllotaxy; sometimes, no branch or just one develops. Mainly the young, lignified nodes of the plagiotropic branches bear fruits.

The purpose of this study was to determine how the architecture of coffee trees affected their yield capacity estimated over two production cycles. We tried to define architectural ideotypes, i.e. coffee trees with good production ability. The ideotype concept has been used primarily by breeders to define a plant model, which then becomes the target of a breeding programme (Dickmann, 1985). An ideotype specifies the ideal attributes of a plant for a particular purpose (Dickmann *et al.*, 1994; Lauri and Costes, 2005). The protocol for studying coffee tree architecture was drawn up with a view to identifying architectural traits capable of predicting tree productivity. These different architectural traits, extracted from an architectural database

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TABLE 1. *Genetic origin of the six clones used in the study*

Clones	Origin	Genetic group
587, 588	$181 \times A03$	Between-group × Congolese hybrid
119, 126, 305, 461	Selected in plantations	Guinean, Congolese between-group hybrids

created for *C. canephora*, were tested as descriptors of the yield capacity of trees. The heritability of the architectural traits was therefore estimated, and the ability of those traits to predict yields was tested.

MATERIALS AND METHODS

Plant material

The plant material observed consisted of six clones of *Coffea canephora* Pierre planted within a trial comparing 20 clones in a totally randomized single-tree plot experimental design. The trial was planted at the CNRA (Centre National de la Recherche Agronomique) experimental station at Divo, Ivory Coast in 1987. The genetic origin is indicated in Table 1 in accordance with the known genetic diversity of *C. canephora*, which comprises two major genetic groups, Guinean and Congolese, whose hybrids display group heterosis (Berthaud *et al.*, 1984; Leroy, 1993). The planting density corresponded to 1667 plants per hectare, i.e. a spacing of 3×2 m. The coffee trees came from cuttings and were free-growing on three stems. Mineral fertilization complied with the recommendations of extension services.

Tree yield was measured annually. Yields cumulated over the first cycle (4 years' production: from 1989 to 1992), over the second cycle (5 years' production: from 1994 to 1998) and over the entire nine years were calculated and expressed in kilograms of green coffee per hectare.

Architecture study protocol

Plant architecture is a relatively recent discipline (Hallé *et al.*, 1978), for which the first quantitative modelling operations were actually carried out on coffee (De Reffye, 1979; De Reffye *et al.*, 1990). The geometric, topological and spatial organization of the plant's entities define its architecture (Godin, 2000). This architecture develops over time, in line with growth dynamics that depend on the genome of plants and on the environmental conditions in which they grow.

Architectural observations on coffee trees were defined with a view to developing databases that were as comprehensive as possible (Godin, 2000). This methodology was based on multiscale representation of plants (Godin and Caraglio, 1998). A plant is a branching system consisting of different elementary organs (nodes, internodes, leaves, fruits) for which the sequence, geometry and spatial arrangement are organized. This organization results from an organogenesis process that continues throughout the lifetime of the plant. Studying the organizational levels of a plant amounts to studying the apical growth and branching

processes. The ability to reproduce certain functioning phases is responsible for the extremely repetitive nature of plant structures, reflected in the organization of plants in 'modules' (Harper *et al.*, 1986). Description of the adjacency of these modules corresponds to the 'topological structure' concept. A topological structure can usually be represented by a graph in which the vertices (summits) represent the modules, and the arcs (each arc being represented by a pair of summits) symbolize the adjacency relations between modules. In this study, coffee tree architecture was studied on a node scale, which thus constituted the basic observation module. Most plant representations in modelling are 'tree diagrams', i.e. connected graphs possessing particular properties (Godin and Caraglio, 1998). Given the dual process of apical growth and branching, two types of adjacency between the entities of a plant are distinguished:

1. the entities were produced by the same meristem (the arc linking the two entities is labelled with '<');
2. one of the entities was produced by a meristem that was axillary to the other (the linking arc is labelled with '+').

Lastly, each node may be linked with information about the geometry and properties of the associated entity (e.g. its dimensions).

Architectural observations were therefore carried out on six clones of the species *Coffea canephora* during the second cycle in May 1997. On average, 28 trees were observed per clone, i.e. a total of 167 coffee trees. The trees were grown in a 3-stem system and one stem was sampled per tree.

The sampled stem per tree and the plagiotropic branches taken at certain levels of the stem were described node by node. The reason for describing the stems was to detail their branching structure and their geometry. Branching was described by the sequence of the number of branches per node starting from the top of the stem down to its base. The first node identified at the top corresponded to the first node bearing branchings. This reference point was a uniform criterion for synchronizing observations. The geometry of each stem was described by measuring the diameter at its base (at ground level) and by different diameters measured along the stem; stem height, from the ground to the apical reference point (short internode corresponding to the latest slowdown in plant growth) was also measured. Diameters were always measured at the widest point of the internode. The geometric traits of the stem at the top of each zone were determined by measuring the height and diameter of the stem's nodes at levels 5, 15, 25 and 35, starting from the top of the tree.

The plagiotropic branches of the same levels (5, 15, 25 and 35) or of the nearest levels, when branches were missing from those levels, were sampled. For each branch (two at most) the sequence of nodes forming the branch were noted, indicating the following for each node:

the number of leaves present on the internode (0,1,2);
the existence or absence of flowers or fruits (0,1);
the existence or absence of secondary branching (twigs): for each twig, the total number of leaves and fruiting nodes it bore were recorded;
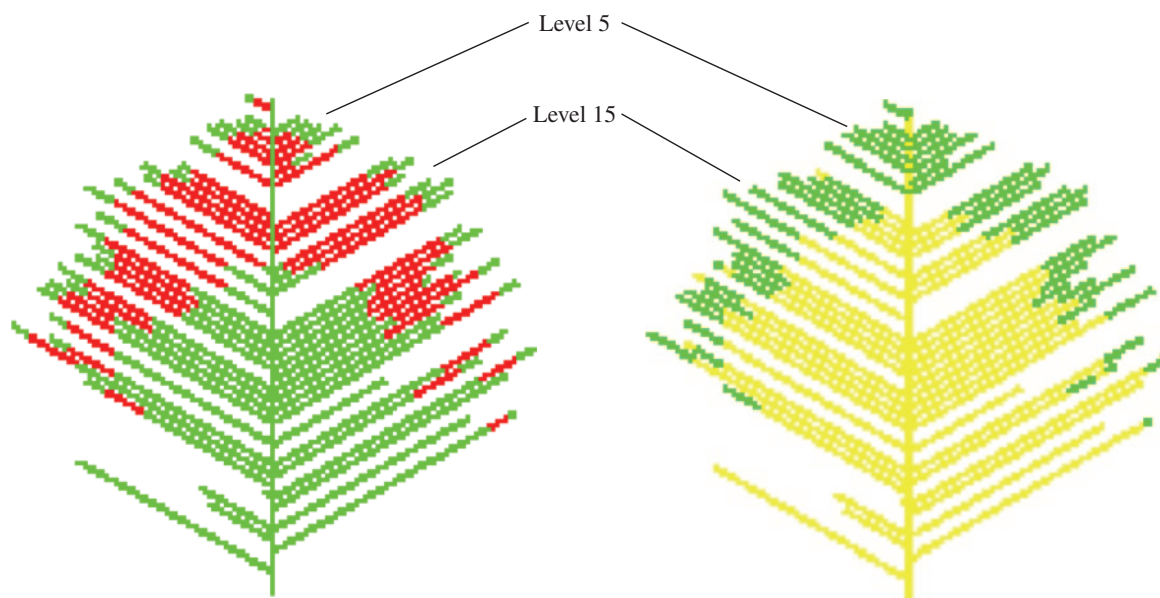
FIG. 1. Diagrammatic representations of one stem of the clone 588. In the image on the left, fruit-bearing nodes are shown in red. In the image on the right, nodes with either one or two leaves are shown in green.

the condition of the branch tip (dead or alive);
the total length of the branches (in cm).

The data were collected in a format compatible with AMAPmod, a software specialized in exploring architectural databases (Godin *et al.*, 1997, 1999).

One stem of a tree belonging to the clone 588 was exhaustively observed in order to visualize schematically the stem's structure (Fig. 1).

Constitution of an architectural database

The database contained the 167 observed stems. It contained around 25 000 described entities and could be used to display certain parts of the plant and extract architectural traits that could then be used as yield predictors. Part of plant 81 is shown in Table 2 as an example. Only the first plagiotropic level (stage 6) is covered by the table. The database also contained information about levels 15, 25, 37 and 45.

By carrying out different extractions, quantitative traits were obtained per tree (number of nodes on the stem, number of plagiotropic branch nodes at different levels, number of fruiting nodes at the different levels, number of leafed nodes, etc.). Once extracted from the database, these traits were correlated with the different cumulated yields available, in order to find yield predictor traits.

Choice of architectural traits

It was possible to extract a very large number of architectural traits from this database. Subsequently, we selected relevant traits, i.e. those that clearly defined tree shape, tree growth and, if possible, their yield capacity. Many traits were extracted and analysed, but we shall only be describing here those traits that were most representative of differences between the clones studied.

Orthotropic stem:

stem (trunk) length (*Ht*), (in cm);
number of nodes on the stem (*Nno*);
average length of internodes on the stem (*Lin*), (in cm).

Plagiotropic branches:

average number of nodes at levels 5 and 15 (2 branches per level), (*Nno5*, *Nno15*);
average number of fruiting nodes at levels 5 and 15, (*Nfrno5*, *Nfrno15*);
proportion of fruit-bearing nodes at level 15, (*Pnofru15*);
average number of leaves per node at level 15, (*Nlea15*);
average length of the branches at levels 5 and 15, (*Leng5*, *Leng15*), (in cm);
average length of the internodes at level 15 (*Lin15*), (in cm);

Plagiotropic/orthotropic:

squatness of the trees (dimensions), (*Squat = Leng15/Ht*);
squatness of the trees (in number of nodes), (*Squatin = Nno15/Nno*).

Data analysis

The REML method (Corbeil and Searle, 1976) was used to estimate the different variances ('clone' and 'error' variances) for the different traits. Broad-sense heritability values were evaluated for the traits, along with the associated confidence intervals, estimated by the Wald method (Agresti and Coull, 1998). Estimations of heritabilities were given by the ratios of genetic variances ('clone' variances)

TABLE 2. *Sample of plant 81 in the architectural database*

Plant	NBranch	NLeaves	Nnofru	State	Length	Diameter	Clone	Line	Tree
/P81							119	222	8
/A1						38			
/E46									
<E45	1			R					
<E44									
<E43									
<E42									
<E41	1			R					
<E40									
<E39	1								
<E38									
<E37	2			R	93	22			
<E36	1								
<E35									
<E34	2								
<E33	1			R					
<E32									
<E31	1			R					
<E30	1			R					
<E29	1			R					
<E28									
<E27	1								
<E26	1			R					
<E25	2				122	16			
<E24	1			R					
<E23	2								
<E22	2								
.									
.									
<E7	2								
<E6	2				192	8			
+A1					21	5			
/E1		2	1						
<E2		2	1						
<E3		2	1						
<E4		2							
<E5		6							
+A2					21	4			
/E1		1	1						
<E2		2	1						
<E3		2							
<E4		2							
<E5		6							
<E5									
<E4		2							
<E3		2		S					
<E2		1		S					
<E1		2		S					
<E0		10			197	6			

and phenotypic variances (Falconer, 1974):

$$h_b^2 = \frac{\sigma_G^2}{\sigma_p^2} = \frac{\sigma_c^2}{\sigma_c^2 + \sigma_e^2}$$

where h_b^2 = broad-sense heritability, σ_G^2 and σ_p^2 are, respectively, genetic and phenotypic variances, σ_c^2 and σ_e^2 are, respectively, clone and error variances.

The clones were ranked and multiple comparisons of means tests were carried out using the Newman and Keuls method. Genetic and phenotypic correlations were then estimated between heritable architectural traits and cumulated yields. The random model was applied for multivariate analysis, allowing for an estimation of genetic covariances and correlations between these traits (Hill, 1971).

RESULTS

Heritability of some architectural traits and clone classifications

Heritability values are given with confidence intervals at 95 % on the estimations (Table 3). Among the traits related to the main stem, height and number of nodes were the most heritable traits. On the other hand, the average internode length of the stem was not heritable, with a heritability not significantly different from 0. Among the traits related to

plagiotropic branches, the numbers of nodes produced were not heritable traits, whilst the fruiting node proportion, the number of leaves per node and the average length of internodes at level 15 (from the top of trees; Fig. 1) were heritable. Level 15 corresponded to the highest yielding zone of the coffee tree, where branches were a little over one year old. Coffee tree yield in one year was usually borne by nodes emitted the previous year. Some of those nodes bore leaves, whilst the oldest fruiting nodes had already lost their leaves. Tree shape, squat versus slender, was also a heritable trait, thereby making it possible to characterize the clones.

TABLE 3. *Means, broad-sense heritability values and confidence intervals on broad-sense heritability values for the synthetic traits defined (dimensions are in cm)*

Trait	Mean	h_b^2	Confidence interval at 95 %
Ht	243·9	0·489	[0·163, 0·815]
Nno	55·60	0·565	[0·247, 0·882]
Lin	4·40	0·074	[0, 0·199]
Nno5	5·51	0·104	[0, 0·256]
Nno15	14·50	0·235	[0, 0·488]
Nfrno5	1·23	0·089	[0, 0·228]
Nfrno15	10·05	0·246	[0, 0·505]
Pnofru15	0·691	0·283	[0·005, 0·560]
Nlea15	1·24	0·302	[0·015, 0·589]
Leng5	22·06	0·139	[0, 0·322]
Leng15	63·94	0·274	[0·001, 0·548]
Lin15	4·44	0·367	[0·057, 0·676]
Squat	0·267	0·364	[0·054, 0·674]
Squatin	0·266	0·350	[0·045, 0·655]

Means for these traits are given for the six clones studied (Table 4). Clones with large trunks and numerous nodes bore smaller yields than shorter clones. The main stem growth rate was therefore not a favourable trait for yield or, conversely, clones with large yields limited their vegetative growth through competition phenomena (Cilas, 2004). The fruiting node proportion at level 15 (productive level; Fig. 1) was a trait associated with yield cumulated over the two cycles. Squat morphotypes, i.e. those clones whose plagiotropic (fruiting) branch growth was stronger than the growth of the orthotropic stem bearing them, were higher yielders. Although clones 587 and 588 (full sibs) performed very differently for yield, they displayed equal internode lengths.

Correlations of some architectural traits with yield

Some architectural traits were genetically correlated to the yield cumulated over two production cycles (Table 5). Tree-by-tree correlations were also estimated (Table 6). Architectural observations were carried out in 1997. Yet the correlations of these variables with yield were often not optimum with yield in 1997, but with yield cumulated over several years. That result suggests that architectural variables 'approach' the yield capacity of trees better than they do the achievement of a given yield over one year. The fruiting node proportion at level 15—i.e. one of the most productive levels—and the average internode rate appeared to be good predictors of cumulated yield. These results need to be checked on larger populations. The fruiting node proportion and the length of fruiting branches at level 15 were

TABLE 4. *Comparison of clones for architectural traits*

Clones	Y1–10*	Ht	Nno	Pnofru15	Nlea15	Leng15	Lin15	Squat	Squatin
119	480	218·6^c	49·6^d	0·757^a	0·93^d	70·88^a	4·89^a	0·326^a	0·297^a
588	449	214·5^c	50·5^d	0·751^a	1·21^{bc}	61·00^{bc}	4·10^d	0·287^b	0·301^a
461	414	268·8^a	63·6^a	0·757^a	1·12^c	65·70^{ab}	4·57^{bc}	0·247^c	0·228^b
126	350	261·4^a	57·6^b	0·674^a	1·40^{ab}	71·97^a	4·38^c	0·278^b	0·288^a
305	308	265·1^a	59·4^b	0·692^a	1·56^a	55·32^c	4·66^b	0·211^d	0·202^b
587	201	241·2^b	53·7^c	0·514^b	1·25^{bc}	58·00^c	4·04^d	0·241^c	0·270^a

Multiple comparison of means tests; means followed by different letters are significantly different (Newman–Keuls at 5 %).
* *Y1–10*, cumulated yield over the first two cycles.

TABLE 5. *Genetic and (in brackets) environmental correlations between architectural traits and yields over different periods*

	Y1c	Y2c	Y1–10	Y97
Ht	−0·577 (0·203)	−0·009 (0·402)	−0·302 (0·341)	−0·039 (0·200)
Nno	−0·302 (0·224)	0·038 (0·384)	−0·130 (0·344)	0·025 (0·225)
Pnofru15	**0·884** (0·091)	**0·887** (0·052)	**0·993** (0·082)	**0·901** (0·102)
Nlea15	−0·697 (0·019)	−0·265 (0·044)	−0·532 (0·036)	−0·329 (0·073)
Leng15	0·265 (−0·003)	0·732 (0·081)	0·613 (0·043)	0·636 (0·103)
Lin15	0·200 (−0·214)	**0·857** (−0·172)	0·663 (−0·221)	**0·918** (−0·119)
Squat	0·601 (−0·112)	0·580 (−0·128)	0·690 (−0·137)	0·539 (−0·013)
Squat	0·342 (0·009)	0·103 (−0·011)	0·243 (−0·001)	0·024 (0·054)

Figures in bold indicate a significant correlation at 5 % level.
Y1c, Yield cumulated per tree over the first 4 harvest years (1st cycle); *Y2c*, yield cumulated over the 2nd cycle; *Y1–10*, yield cumulated over both harvest cycles; *Y97*, yield in 1997 (year of the architectural observations).

TABLE 6. *Phenotypic correlations (tree-by-tree) between architectural traits and yield over different periods (with associated probability in brackets)*

	Y1c	Y2c	Y1–10	Y97
Ht	−0·062 (0·261)	0·180 (0·001)	0·073 (0·186)	0·036 (0·516)
Nno	0·154 (0·004)	0·157 (0·004)	0·180 (0·001)	0·027 (0·616)
Pnofru15	0·244 (0·001)	0·369 (<0·001)	0·355 (<0·001)	0·423 (<0·001)
Nlea15	−0·159 (0·038)	−0·105 (0·170)	−0·151 (0·048)	−0·117 (0·127)
Leng15	0·002 (0·968)	0·258 (<0·001)	0·185 (0·015)	0·242 (0·001)
Lin15	−0·096 (0·210)	0·189 (0·013)	0·058 (0·448)	0·246 (0·001)
Squat	0·073 (0·343)	0·127 (0·103)	0·116 (0·134)	0·201 (0·009)
Squatin	0·098 (0·201)	0·032 (0·670)	0·074 (0·332)	0·050 (0·519)

also correlated to cumulated yields on a tree scale (phenotypic correlation, Table 6).

It is therefore possible to bring out morphotype tendencies for yields, but those morphotypes may not be unique and several architectures may be conducive to fruit production.

DISCUSSION

Architectural traits were measured on coffee trees from a clonal trial and a database usable with AMAPmod software was created. Of the few traits tested, the average fruiting node proportion at level 15 from the top of the tree displayed significant genetic correlations with cumulated yields. The genetic correlation was higher with yields cumulated over the 9 years than with the yield of the individual year observations. The average numbers of fruiting nodes at the most productive levels would therefore seem to represent a yield potential which can only be realized over a large number of years. A larger average internode length on plagiotropic branches at the fruiting levels also appeared to be a conducive trait that needs to be confirmed. Other architectural traits will have to be tested in order to quantify competition phenomena between fruit production and vegetative growth.

From this work, it has thus been possible to determine architectural ideotypes, i.e. cultivars with morphology and growth that are conducive to their cultivation and yield. Similar studies are under way in a *C. arabica* diallel mating design, in order to generalize this architectural ideotype concept. Determining architectural ideotypes will also amount to identifying 'efficient' coffee tree shapes. As shown with apple (Lauri *et al.*, 1995; Costes and Guédon, 1997), tree shape could be a first step to understanding the relationships between tree growth, branching and fruiting. In plants, an efficient shape should make it possible to optimize certain physiological functions (Farnsworth and Niklas, 1995). This idea of an optimum shape has been generalized to the living world as a whole and is known as the constructal theory (Bejan, 2000). This theory suggests that optimum shapes are associated with particular physical or biological functions, and that those natural shapes are determined by an optimum distribution of imperfections. For instance, the branches and roots of a tree must give it access to maximum resources in the air and soil. Plant shapes would seem to be merely the result of ongoing adjustments in relation to the environment and would appear to structure themselves as they occur (Poirier, 2003). In this structuring, the genome is considered as the initial motif of a self-organizing process, the first building block in forming growth (Kupieck and Sonigo, 2000). Starting from a given genome, the shape of a plant would therefore seem to be the result of a morpho-dynamic process that optimizes hydraulic exchanges and gas exchanges depending on environmental conditions, for optimum yield (Pearcy *et al.*, 2005). In crop plants, optimum yield may be a total biomass yield, or leaf, root, fruit or seed yields, depending on which organs are of economic interest. For coffee, it would therefore be a matter of determining which shapes lead to an optimized fruit yield that is stable over time and competes as little as possible with vegetative growth as regards the number of nodes produced. Competition with other coffee trees in a given plantation system can also be reduced by selecting low-competition genotypes (Montagnon *et al.*, 2000). Breeders would therefore need to choose the most appropriate architectures capable of sustainably producing in given environments those products for which the plants are grown. It would also be a matter of finding out whether several shapes can give the same results, i.e. determining whether one optimum shape or several optimum shapes exist for a particular plant species.

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